The Interrelationships of Certain Boreal and Arctic Species of *Yoldia* MÖLLER, 1842

BY

I. McT. COWAN

University of British Columbia, Vancouver, British Columbia, Canada

(Plate 5; 9 Tables)

MEMBERS OF THE PROTOBRANCH genus *Yoldia* are among the most widely distributed Lamellibranchia in northern oceans. They inhabit mud bottoms to depths of 100 fathoms ± and may be the most abundant mollusk on them. Their abundance in the stomachs of bottom-feeding fishes suggests that they are an important element in the benthic food chains.

Within this genus there is a group of species characterized by the simultaneous presence of an elongate form with tapered, sub-acute posterior extremity, an approximately central umbo, slender rather than bulbous form, a highly polished cuticle devoid of sculpture or surface pattern of any kind, and with an unstriated resilifer.

Several names have been applied to members of this group:

Yoldia amygdalea VALENCIENNES, 1846, described from specimens obtained on the cruise of the '*Venus*' at Kamchatka.

Yoldia hyperborea (LOVÉN) TORELL, 1859, was described on the basis of specimens from Spitzbergen.

Yoldia limatula gardneri OLDROYD, 1935, from Garden Bay, Pender Harbour, British Columbia.

Yoldia limatula (SAY, 1831) was based upon specimens taken in fish stomachs in Massachusetts waters.

Yoldia norvegica. DAUTZENBERG & FISHER, 1912 regarded the specimens from the coast of Norway as distinctive and applied this name, without designating a holotype.

Yoldia hyperborea limatuloides OCKELMANN, 1954, is the most recent name to appear. The type locality is Fossfjord, N. W. Iceland, but the form is stated to occur also from the Lofoten Islands to eastern Finmark.

All have been described from shell characters alone and in only one instance (OCKELMANN) has an attempt been made to express the observed differences quantitatively. He used 3 shell ratios in an attempt to distinguish *Yoldia limatula, Y. sapotilla* and *Y. hyperborea* and found them to be of little use.

One of the problems of developing quantitative expression of difference in the form of the lamellibranch shell is that in most species it grows throughout life. In many species also the shell changes in proportions with growth and thus renders dimensional ratios meaningless. This leaves the possibility that in any comparison of shell dimension between different populations the bias due to age or size may be great.

In the present study I have attempted to avoid this problem by regressing pairs of measurements so as to develop an expression of the relative growth of the different parts of the shell in each apparently distinct population. Analysis of covariance was used in making mathematical comparison between the equivalent regression coefficients of different populations.

In order to develop these criteria my series for measuring were selected to contain the widest possible size range from each locality.

METHODS

Samples from individual geographic locations were given close visual inspection followed, in some cases, by trial comparison of ratios. Where no or almost no differences were apparent, the samples were pooled into composite samples suspected of representing definable entities of possible taxonomic value. Greatest length of the shell has been used as the basis of each regression. While the slope of the regression line is certainly a biologically meaningful expression, the position of the intercept on the Y axis is probably no less a characteristic of the population. Its biological meaning, however, is less apparent.

All statistical procedures were undertaken on a digital computer.

MEASUREMENTS

All measurements were taken with a sliding caliper equipped with a dial vernier. The measurements taken and the symbols employed to designate them on the analytical tables are as follows:

X = The greatest length of a single valve taken in a straight line. Left and right valves were measured in each instance where they were available and intact.

Y1 = The greatest height of the valve from ventral margin to peak of the umbo taken at right angles to the dorsal plane.

Y2 = The length of the pallial sinus measured from the posterior tip of the shell.

Y3 = The anterior length of the valve taken from highest point on the umbo to the most distant point on the anterior margin.

Y4 = The posterior length measured similarly.

Y5 = The number of teeth on the posterior side of the umbo.

Y6 = The number of teeth on the anterior side of the umbo.

Y5 + Y6 = thus the total number of teeth on the hinge line.

The small teeth close to the resilifer were difficult to count on certain large specimens but every effort was made to expose them and count them accurately.

POPULATIONS SELECTED FOR COMPARISON

The selection of populations to be compared statistically is a critical step in the process of exploring for significant differences. I know of no substitute for careful visual inspection of the field samples supported by trial comparison of measurements and this has been the basis of selection used here. It was felt to be important to include for comparison those populations that had been previously described as differing from others, along with those that the present study revealed. Thus the following stocks have been treated separately.

1. The form inhabiting the high Arctic seas around the world.

2. The population of Kamchatka, the southwest Bering Sea and the Sea of Okhotsk.

3. The population from Iceland and the coast of Norway.

4. The population inhabiting the western Atlantic from Nova Scotia to Massachusetts.

5. A small collection from depths of 155 - 285 fathoms in Delgado Canyon, off Cape Mendocino, California. This population appears to be discontinuous from others, both geographically and by depth occupied.

6. The specimens from the coast of Alaska south of the Alaska Peninsula.

7. The many localities represented in Georgia Strait, British Columbia.

8. A sample from Malcolm Island, Queen Charlotte Strait, British Columbia.

9. A sample from Masset Inlet, Queen Charlotte Islands, British Columbia.

At the same time some local variation seemed apparent along the coast of British Columbia where barriers to free dispersion seemed to be few. To explore the nature of variation under these circumstances, 3 populations (7, 8, 9) were included in comparison with specimens from the contiguous areas along the Alaskan coast.

COMPARISONS

Tables 1 to 6 present the results of covariance analysis derived from the regressions obtained from the 9 populations. For purpose of interpretation I have used .01 as the level of significance to which systematic meaning can be attached.

Let us first examine the several samples drawn from the relatively continuous north-south distribution along the coast of British Columbia and southeastern Alaska using the centrally placed Masset Inlet population as a basis of comparison (Table 4). Gross inspection suggests that the specimens from the Strait of Georgia are uniformly deeper for their length than those from the other areas. The only exception from this general condition is found in the small series that served as the type lot for *Yoldia limatula gardneri* Oldroyd. These are proportionately shallower, i. e. more slender than the Strait of Georgia form but can be matched among series from the outer coast of British Columbia and Alaska.

It will be seen that the Queen Charlotte Islands stock is identical with the Malcolm Island stock in all slopes of the regressions and differs in only one intercept feature – that is the posterior length. In comparison with the Georgia Strait stock the regression of width on length is different, confirming the general impression referred to above. Two of the intercept figures are different, the pallial sinus scar and the anterior teeth.

The Queen Charlotte Island sample is identical with the Alaskan sample in all features except length – width relationship. It differs from the California sample in two intercept features only.

Table 1

Probability of Significance of Covariance Analysis of Slopes of *Yoldia "norvegica"*

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. hyperborea	+	—	—	—	+	+	+
Y. amygdalea (K) [1]	—	.1	—	.05-.1	—	—	—
Y. amygdalea, Alaska	—	.1-.2	—	.05	—	—	—
Y. limatula, Atlantic	—	—	—	.01-.025	.05-.1	.01-.025	.025

Probability of Significance of Covariance Analysis of Intercepts of *Yoldia "norvegica"*

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. hyperborea	+	+	+	+	+	+	+
Y. amygdalea (K)	.05-.1	—	+	.01-.025	+	.005-.01	+
Y. amygdalea, Alaska	+	+	.001-.005	.005	.025-.01	.025-.01	.01
Y. limatula, Atlantic	.1-.2	—	+	+	.01	+	+

[1] Kamchatka stock

+indicates a probability of accidental occurrence < .001

— indicates a probability of accidental occurrence > .1

Table 2

Probability of Significance of Covariance Analysis of Slopes of *Yoldia hyperborea*

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. amygdalea (K)	+	+	.1	.025-.05	+	+	+
Y. amygdalea, Alaska	+	.001	—	.1-.2	+	+	+
Y. limatula, Atlantic	+	.01	.001	.001-.005	+	+	+

Probability of Significance of Covariance Analysis of Intercepts of *Yoldia hyperborea*

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. amygdalea (K)	+	+	+	+	+	+	+
Y. amygdalea, Alaska	+	+	.01-.005	+	+	+	+
Y. limatula, Atlantic	+	+	.1-.2	+	+	+	+

Table 3

Probability of Significance of Covariance Analysis of Slopes of *Yoldia amygdalea* (K)

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. amygdalea, Alaska	—	—	—	—	—	—	—
Y. amygdalea, Georgia Str.	—	—	—	—	—	.05	.1
Y. amygdalea, California	—	—	—	—	.005-.01	+	+

Probability of Significance of Covariance Analysis of Intercepts of *Yoldia amygdalea* (K)

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. amygdalea, Alaska	+	+	+	+	.025-.05	.2	.05-.1
Y. amygdalea, Georgia Str.	+	.005-.01	+	+	.05-.1	+	.001-.005
Y. amygdalea, Humboldt	—	+	+	.005-.01	.1	+	.1-.2

Thus along the 1000 ± miles of coastline from the Alaskan Peninsula to the coast of California there is a great uniformity in the measurable features of this *Yoldia,* with significant differences in no more than 2 of 14 potential comparisons for any 2 of the sub-populations that gave rise to the samples. These represent a bathymetric range from 10 fathoms to 200 fathoms. The conclusion reached is that the Pacific Coast is inhabited by

Table 4

Probability of Significance of Covariance Analysis of Slopes of *Yoldia amygdalea,* Masset

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. amygdalea, Malcolm Isld.	.1-.2	—	.1-.2	.1-.2	—	—	—
Y. amygdalea, Georgia Str.	+	.05-.1	.1-.2	.05-.1	—	—	—
Y. amygdalea, Alaska	.001-.05	.1-.2	—	—	—	—	—
Y. amygdalea, California	.01-.02	—	—	—	—	.1-.15	.2
Y. amygdalea (K)	.005-.01	—	—	—	—	—	—
Y. norvegica, Norway-Iceld.	.025-.05	.005-.01	—	—	—	—	—

Probability of Significance of Covariance Analysis of Intercepts of *Yoldia amygdalea,* Masset

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. amygdalea, Malcolm Isld.	—	—	.1-.2	.001-.005	.025-.05	.05-.1	.025-.05
Y. amygdalea, Georgia Str.	.025-.5	+	—	—	.1	.001-.005	.01-.025
Y. amygdalea, Alaska	—	—	.025-.05	.1-.2	.1-.2	.05-.1	.05-.1
Y. amygdalea, California	+	—	.1	.001-.005	.2	—	—
Y. amygdalea (K)	+	+	+	+	.2	.05-.1	.1
Y. norvegica, Norway-Iceld.	.001-.005	+	.001-.005	.001-.005	.025-.05	.025	.025-.05

Table 5

Probability of Significance of Covariance Analysis of Slopes of *Yoldia amygdalea* (Bering "Intergrades")

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. amygdalea (K)	.01-.025	.05	.05	—	.01	.001	.001
Y. hyperborea	—	.1-.2	—	—	.025-.05	.1	.05

Probability of Significance of Covariance Analysis of Intercepts of *Yoldia amygdalea* (Bering "Intergrades")

Compared with	Y1/x	Y2/x	Y3/x	Y4/x	Y5/x	Y6/x	Y5+Y6/x
Y. amygdalea (K)	+	.005-.01	+	.05	.1-.2	—	—
Y. hyperborea	+	.05	+	+	+	+	+

a remarkably uniform stock of this species of *Yoldia,* displaying only minor geographic variation in form and in relative growth features. The most obvious of these variants is that occupying the heavily silted bottoms of the Strait of Georgia and Puget Sound.

Table 6 summarizes the differences appearing in the comparisons of the 14 potential differences in numerical attributes that could occur between each of the stocks analysed. If these are arranged to reveal geographic replacement, the Pacific Coast stock differs from that of the Okhotsk-Kamchatka areas in a total of 5 of the indices, Kamchatka from the Arctic stock in 12, the Arctic from Norway-Iceland in 11, and from the American Atlantic coast stock in 13. The number of differences appearing between the Norway-Iceland form and the American Atlantic form is 5.

The Arctic form therefore differs from all others with which it is in contact in 11 or more of the 14 features studied here, whereas none of the other stocks, even those separated by the entire extent of the Arctic Seas, and presently occurring in the North Atlantic and North Pacific, differ in more than 5 features when one uses the .01

Explanation of Plate 5

Figure 1: *Yoldia amygdalea,* Sakhalin Island, NW Pacific. × 1.2
Figure 2: *Yoldia amygdalea,* Masset, Queen Charlotte Island, British Columbia × 1
Figure 3: *Yoldia amygdalea,* Strait of Georgia, British Columbia × 1.6
Figure 4: *Yoldia amygdalea,* California Coast × 1.2
Figure 5: *Yoldia amygdalea,* Iceland × 1.6
Figure 6: *Yoldia hyperborea,* Point Barrow, Alaska × 1.5
Figure 7: *Yoldia hyperborea,* Disco, Greenland × 1.5
Figure 8: *Yoldia limatula,* Eel Pond, Massachusetts × 2

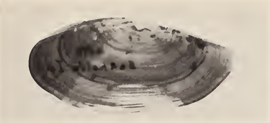

Figure 1

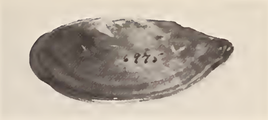

Figure 2

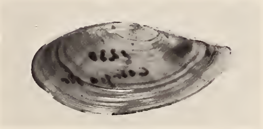

Figure 3

Figure 4

Figure 5

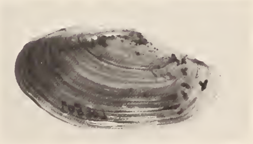

Figure 6

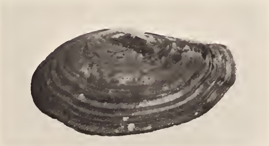

Figure 7

Figure 8

Table 6

Numbers of Features Distinguishing Stocks of *Yoldia*

Comparison	Number of Significant Differences					
	Slope (max. 7)		Interc. (max. 7)		Totals (max. 14)	
	(a) Significant at .01	(b) at .05	(a) Significant at .01	(b) at .05	(a)	(b)
1. Masset : Malcolm Isld.	0	0	1	3	1	3
2. Masset : Georgia Str.	1	1	1	4	2	5
3. Masset : Alaska	1	1	0	1	1	2
4. Masset : California	0	1	2	2	2	3
5. Masset : Kamchatka	1	1	4	4	5	5
6. Masset : Norway-Iceland	1	2	3	6	4	8
7. Arctic : Pacific Coast	5	5	7	7	12	12
8. Arctic : Amer. Atlantic	7	7	6	6	13	13
9. Arctic : Norway-Iceland	4	4	7	7	11	11
10. Arctic : Kamchatka	5	6	7	7	12	13
11. Kamchatka : Norway-Iceld.	0	1	4	5	4	6
12. Norway-Iceland : American Atlantic	0	3	5	5	5	8

level of probability as the criterion of significance. The .05 level of significance does not alter the situation respecting the Arctic population. It is clearly a very different stock. This level, however, reveals the Georgia Strait stock as having more distinctive features than the other samples drawn from the NE Pacific. It also increases the apparent difference between the Norwegian and the American Atlantic stocks.

Returning to the differences at the .01 level (total "a" of Table 6), and comparing geographically contiguous stocks, it is possible to suggest that 3 clearly differentiable stocks exist: (1) that inhabiting the NE Pacific Ocean, the Sea of Okhotsk, the coast of Kamchatka and the southern Bering Sea; (2) the Arctic Seas of both hemispheres; and (3) the shallow waters of the North Atlantic Ocean including Iceland and the coast of Norway. The American Atlantic stock differs from Arctic and Pacific stocks to a similar degree.

The data derived from the covariance analysis of regressions and intercepts reveals the numbers of criteria by which the several stocks differ from one another but tell us little about the nature or direction of the differences. These details can be derived from inspection of the specimens and from the conventional measurements. They do not alter the conclusions to be reached from the present analysis.

Specimens originally from Iceland and the coast of Norway are remarkably similar in general appearance to the specimens taken along the Pacific coast of North America. In fact, the characteristics by which they each differ from the Arctic population (Tables 1 - 4) are in general the same. One might ask, therefore, are they indeed the same organisms separated into the North Atlantic and North Pacific stocks by an inhospitable area of Arctic environment occupied by another form.

A direct comparison between the North Pacific and North Atlantic stocks reveals that, at the .01 level of significance, they do not differ in any of the 7 regressions (Tables 1 & 4), but do so in 4 - 6 of the intercepts, depending upon which Pacific Coast sample is used in the comparison. Clearly then, the differences between the stocks of the two oceans is greater than the differences between any two of the samples from the Pacific coast of North America.

The relationship between the North Atlantic stock and that of the American Atlantic is also interesting. As Ockelmann (1954) pointed out, there are distinct and consistent differences in the shape of the shell between these two stocks. The American Atlantic specimens lack the anterior and posterior indentations in the ventral margin of the shell. There are differences also in the shape of the siphonal muscle scar. My data suggest two features of shell proportion and dentition ($p < .025$) and 5 intercept characteristics that distinguish the two Atlantic stocks.

The general form of the North Atlantic specimens suggests that they might be the outcome of intergradation between the Arctic form and that of the American Atlantic. Their geographic situation and the absence of any substantial evidence of intergradation along the coasts of Newfoundland and Labrador leave us with no evidence to support such an explanation. I have seen no series of *Yoldia* from Newfoundland and Labrador, so future collections may require a re-examination of the relationships between the 3 forms encroaching upon the North Atlantic.

TAXONOMIC CONSIDERATIONS

It has been shown that there are few differences between several stocks of *Yoldia* separated widely along the Pacific coast of North America. It has also been shown that these do not differ substantially from the form inhabiting the Sea of Okhotsk and the Kamchatka coast. The first available name for this stock is *Yoldia amygdalea* Valenciennes, 1846.

The name *gardneri* Oldroyd, 1935, applied to a supposed subspecies of *Yoldia limatula* (now *Y. amygdalea*) in the northern part of the Strait of Georgia, British Columbia, appears to be without foundation. It referred to unusually slender examples that occur among the normal population.

Yoldia hyperborea (Lovén) Torell, 1859 is the accepted name applicable to the distinctive and remarkably uniform stock of Arctic Seas.

In my opinion, the characteristics of the stock from the North American coast of the Atlantic, taken with the absence of certain evidence of intergradation with *Yoldia hyperborea* to the north argue for recognizing this as a separate species under the name *Y. limatula* (Say, 1831), that has been used for this form for more than a century.

Ockelmann (1954) regarded the form of the North Atlantic as a subspecies of *Yoldia hyperborea* and applied the name *limatuloides* to it. It has now been shown that this population differs as profoundly from *Y. hyperborea* as any of the other stocks compared. The weight of evidence now suggests that this stock be regarded as conspecific with *Y. amygdalea* and that this species, as is the case with *Y. myalis,* is now divided into Atlantic and Pacific stocks differing but little from one another. If a subspecies designation be regarded as useful, the name *Y. norvegica* Dautzenberg & Fischer, 1912, though not described with a designated type specimen, was clearly applied to the form of the Norwegian coast and has priority over *limatuloides* of Ockelmann. This author regarded *Y. norvegica* as a synonym of *Y. hyperborea,* but the geographic reference by Dautzenberg & Fischer seems to deny this. In this instance there seems to be no need for a separate designation for this stock.

It is pertinent to ask whether there is any strong evidence of intergradation between stocks I have defined as possessing characteristics suggesting clear cut differences. Thirteen specimens from the eastern Bering Sea (St. Matthews Island, Nunivak Island, N of Unimak Island, near Pribiloff Islands) originate from an area where intergradation between *Yoldia hyperborea* and *Y. amygdalea* might be expected to occur. They do indeed show characteristics of form apparently intermediate in some degree. Table 5 presents the probabilities of significance of covariance analyses comparing the possible intergrades with both the putative parent stocks. While *Y. amygdalea* differs from *Y. hyperborea* in 12 criteria, it differs from the supposed intermediates in 5 and *Y. hyperborea* differs from them in 6. The differences are in the expected direction.

On the strength of these comparisons, and others involving unmeasurable aspects of shell form there seems to be evidence that these specimens are indeed intermediates between the Arctic and North Pacific-Kamchatka forms. The question then arises as to the interpretation to be placed upon this intergradation. It could be regarded as evidence that complete introgression is possible and that the two populations should be regarded as subspecific expressions of a single wide ranging species.

In the genus *Yoldia, Y. myalis* and *Y. thraciaeformis* both occur in twin populations occupying the North Pacific and North Atlantic and separated by the Holarctic region in which they do not now occur. In this study evidence is produced to reveal *Y. amygdalea* as similarly distributed. The first two species named have no surviving close relative in Arctic waters. One can conclude, therefore, that they previously occupied Arctic waters but have been exterminated in them so recently that little or no morphological difference has developed between the relict populations. The failure of the Arctic stocks may well have occurred during the closure of Bering Straits, with the considerable alteration in the circulation of Arctic waters and possibly of local mid water habitats. A possible alternative explanation would involve continuity of distribution through tropical waters at a time when the two Americas were separate. This seems less likely.

In the case of *Yoldia amygdalea* rather than extermination, evolutionary change gave rise to a form adapted to arctic conditions (*Y. hyperborea*). The evidence of the samples now available from the southern Bering Sea suggest that genetic isolation between the two species is incomplete. It seems to me, however, that the existence of the North Atlantic stock of *Y. amygdalea,* the very extensive range of this species in the Pacific, the extent of the area occupied by *Y. hyperborea* in the Arctic, and the absence of any evidence of intergradation between it and the Atlantic *Y. amygdalea* all point to species status as best expressing the relationship between *Y. hyperborea* and *Y. amygdalea* despite the evidence of some introgression over a narrow area of contact in the Bering Sea.